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THE EVOLUTION OF HOMINID BIPEDALISM

ABSTRACT: *In the Laetoli footprint site G three hominid trails are intersected by two Hipparion-trails. These trails give additional information on the locomotion of the first bipedal hominids and the tridactyl horse. There is a general consensus on the significance of the tridactyl tiptoe gait in horses. This gait was an essential step in the evolutionary history of the horse to enter the open plains. It procured the animal with a locomotion that combined speed and endurance. The Laetoli Hipparion-trail shows that, compared with the monodactyl horse, the tridactyl horse was more all-round in locomotion.*

The hominid trail, probably from Australopithecus, is clearly that of a bipedal locomotion, but there is no consensus on its interpretation among scientists. Australopithecus was the first to enter the open plain and had just as Hipparion a more all round gait than Homo. Compared to the hominid evolutionary history with that of the horse, it shares a similar evolutionary pattern, which leads us to the conclusion that the hominid pattern is not unique and must be explained as other mammals. The bipedal locomotion was essential to enter an open plain. Compared to Homo, Australopithecus had a more all-round gait.

KEY WORDS: *Bipedalism – Hominids – Equids – Evolution*

INTRODUCTION

In the Laetoli footprint site G three hominid trails are intersected by two *Hipparion*-trails (*Figure 1*). The *Hipparion* foot-prints give an answer on a long dispute between paleontologists, namely the question if the laterals of this tridactyl horse were functional. The two *Hipparion* trails are probably related to that of a mare with a foal, travelling at moderate speed in a single foot gait. The smaller foal extended its legs slightly more and moved them relatively faster to held up with its mother (Renders 1984, Renders, Sondaar 1987). When the trackway of the foal crosses that of the mare, the mother slipped with her left front leg and it shows that the right hind laterals touch the ground, giving the animal extra support on the slippery soil. In consequence it can be argued that the laterals of

the tridactyl unguligrade horse (*Hipparion*) are functional, given the animal extra support when needed. Compared to the monodactyl horse, the locomotion of the tridactyl horses is more all round.

If we consider the hominid footprints at Laetoli (Johanson, White 1980), than there is no general consensus on their interpretation. They are explained as strikingly like footprints of *Homo sapiens* (e.g. Clarke 1979, Leakey, Hay 1979, Day, Wickens 1980, White 1980, Capecchi 1984, Robbins 1987, White, Suwa 1987, Tuttle 1985, 1987, 1988, 1990, 1994, Tuttle *et al.* 1990, 1991a, b, 1992).

Stern and Susman (1983) in contradiction think that they spot several features that are more characteristic of chimpanzee footprints than of human ones. Tuttle (1985, 1996) rebutted all of their points and censured their unsystematic approach to casts of the prints and selective



FIGURE 1. The Laetoli footprint site G with hominid trails which are intersected by two *Hipparion*-trails.

observations on chimpanzee and human footprints. Clarke (1985) and Deloison (1991, 1992) believed that the individuals of particular prints had long toes, which fits in a chimpanzee pedal model. Tuttle (1996) found no support for Deloison's (1991, 1992) chimpanzee pedal model for the Laetoli G hominids.

In general the footprints are attributed to *Australopithecus afarensis* (e.g. M. Leakey 1995, Wolpoff 1996). However, Tuttle (1996) stated that the footprints cannot be accommodated in *Australopithecus afarensis* on the basis of pedal morphology. According to Tuttle (1996) *Australopithecus afarensis* is characterized by apish curved toes that are unlikely to produce virtually human footprints (Tuttle 1988, Tuttle *et al.* 1990, 1991a,b).

So, the trackway of the *Australopithecus* is not as conclusive, but there are enough arguments to conclude that *Australopithecus* was bipedal, but did not have the striding gait like modern man. Also here we can make the conclusion that this hominid had a more all-round gait.

In both – horses and hominids, there is a rapid evolutionary shift in locomotory apparatus, when they move from forest to open plain. However, the significance of this evolutionary response to entering a new environment is evaluated in a different way. In the horse we find the general consensus under specialists. The tridactyl tiptoe locomotion is considered to be essential for entering the new environment, an open plain, as it procured the animals with a locomotion that combines speed and endurance. It is considered as a typical example of a pioneer structure (Spaen *et al.* 1994, Sondaar 1994).

In the hominids there is not any consensus in explanation; some of the existing "hypotheses" about the origin of hominid bipedalism are:

- savannah-dwelling (e.g. Darwin 1871);
- carrying (e.g. Hewes 1961, Kortlandt 1967); ancestors adopted the erect position to carry food (e.g. Leakey, Lewin 1979);
- generalized social cooperation with "autocatalytic" feedback (e.g. Darwin 1871, Lovejoy 1981);
- adoption by small-brained hominids of a socio-reproductive system involving food sharing, provisioning and central place foraging (e.g. Hewes 1961, Washburn 1965, Isaac 1978, Lancaster 1978);
- gathering (e.g. Zihlman, Tanner 1979, Tanner 1981); to gather berries hanging at the top of the shrubs (e.g. Pilbeam 1980); feeding adaptations (DeBrul 1962, Jolly 1970, Leutenegger 1987);
- tool-making (e.g. Washburn 1950, 1960, 1967); use of tools and weapons (e.g. Darwin 1871, Tobias 1967, 1981, Washburn, Moore 1980), to be able to throw stones;
- predation (e.g. Ravey 1978); hunting (e.g. Darwin 1871, Dart 1925, 1953, Ardrey 1961, Washburn, Lancaster 1968);
- display (e.g. Livingstone 1962), to show their sexual attributes; to look taller and more fearful to adversaries; to see over tall grass; better vision;
- thermoregulation (e.g. Wheeler 1984, 1985), to reduce exposition of the body to the sun;
- bioenergetics (Tayler, Rowntree 1973), for mechanical and energetic reasons due to a change in diet;
- to stand up in the water (Hardy 1960, Morgan 1972, 1982).

The list is long and may easily be expanded, however, not even one of these explanations can be unambiguously confirmed at the moment. Some are plausible, others less so. Most are concerned by freeing the hands.

The fact that bipedal locomotion provides *Australopithecus* with an energy saving apparatus which gives endurance, a need for surviving in the open environment, just as the tridactyl tiptoe locomotion in *Hipparion*, is not mentioned in the first place. This gives rise to the question: "Is human evolution unique and does it need to be explained in a different way, compared to that of other mammals?" or "Are paleo-anthropologists influenced by the fact that they study the evolutionary

history of their ancestors and do they treat paleontological data in a different way than paleontologists?"

The only way to answer these questions is to reconsider the fossil record of the hominids and analyse the evolutionary changes just as in other mammals. We have chosen in this paper to compare the hominid evolution with that of the horse, because:

1. The fossil record of the horse family is surprisingly complete and demonstrates an evident relation between changes in functional structures and changes in environment;
2. Horse and human locomotion are better studied, and their functional morphology is better known than any of the other mammals. This enables us to give a more realistic reconstruction of the locomotion from the fossil genera. Besides this the fossil footprints in Laetoli give additional information.
3. The coincidence that the footprint tracks of tridactyl horse (*Hipparion*) and *Australopithecus* intersect each other at footprint site Laetoli G. These tracks are still not fully those of the recent horse and of modern man. They both represent a more "all-round" foot, an important evolutionary step in evolving their actual stage: *Homo sapiens* and *Equus caballus*.

HORSE EVOLUTION: FROM FOREST TO THE PLAINS

The change of habitat from a forested to an open environment in mammals is reflected in morphological changes in the skeleton, which are adaptive. This is especially clear in the herbivore locomotion, which became more digitigrade; an elongation of the lower parts of the limb, resulting in walking on the toes with stretched legs. In the fossil record of the horse these adaptive changes are well documented and it can be demonstrated that different functional structures, locomotory and masticatory apparatus, change according to different, in time and rate, evolutionary patterns.

Locomotion (Figure 2)

A. *Hyracotherium*

Hyracotherium has four toes on the front foot and three on the hind foot. The foot has a distinct pad. The lateral toes can move separately. The particular characteristic of the equid locomotory apparatus was already evolved, namely a padded ungulate odd-toed foot and somewhat elongated metapodials. In other words, the distal elements of the limbs are lengthened relative to the proximal ones. Thus, there is lengthening of the limb, while the centre of mass remains situated proximal and its inertia is reduced.

B. *Mesohippus-Anchitherium-Hypohippus* are tridactyl. The laterals always touched the ground and were functional in resting position too. The phalanges are short, the foot

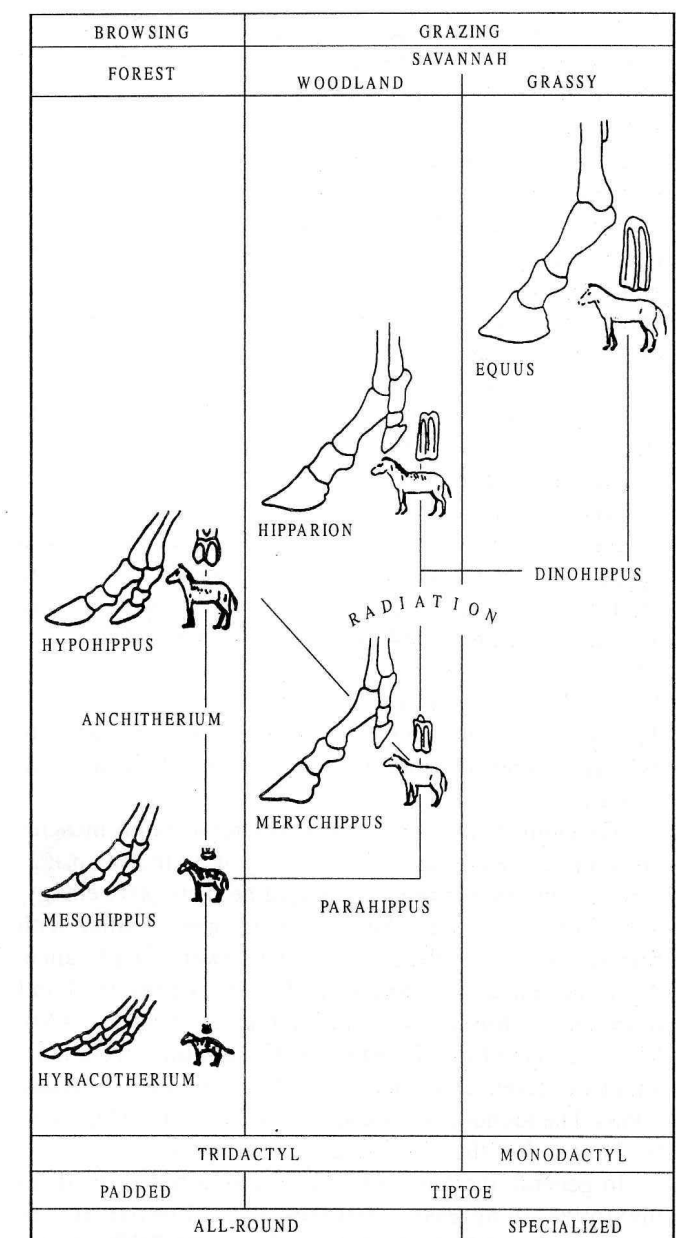


FIGURE 2. In the evolution of the horse we can observe a change from the browsing woodland horse with low-crowned teeth and a padded tridactyl foot to the grazing savannah horse with high-crowned teeth and a tridactyl tip-toe foot. In the tridactyl grazing horses with a tip-toe foot a radiation took place. This led among others to the first monodactyl horse *Dinohippus*, the ancestor of the modern horse *Equus* (after Sondaar 1994).

has a distinct pad. The padded sub-unguligrade foot of the horse combines a cursorial adaptation with mobility, which is important in a forest or open forest to move around obstacles. A main difference in comparison with *Hyracotherium* is that the metacarpals and radius/ulna function as one element by a carpal blocking mechanism. This lineage of horse (*Mesohippus-Anchitherium-Hypohippus*) can be followed up to the Late Miocene.

C. Parahippus-Merychippus-Hipparion are tridactyl.

In the Early Miocene a new, more successful group, evolved in North America – the grazing horses. This change in evolutionary direction coincides with the spread of grasses at that time (e.g. Simpson 1951, Stebbins 1981). The horse entered a new environment, the plains. A major change can be noted in the foot. The subunguligrade padded foot changed into the true unguligrade tridactyl foot. There is elongation of the first phalanx, causing the lateral toes to come free from the ground. Larger mobility is noticed in forward and backward motion.

This change in locomotory system occurred as a rapid shift from one mechanical type to the other. Intermediate steps are not found in the fossil record and therefore it is called a pioneer structure (Spaan *et al.* 1994, Sondaar 1994). *Parahippus* is the first horse with this type of locomotion which was very successful as it can be followed up till the Pleistocene. Essentially it was much like the modern horse, but its functional lateral toes made it more all-round (Renders 1984, Renders, Sondaar 1987).

D. Dinohippus-Equus are monodactyl.

The last major change in locomotion is seen in the Late Miocene, when the monodactyl horse evolved in North America.

The elongation of the phalanx is extreme. Some muscles "tendonize", resulting in the forming of a kind of spring-mechanism comparable to a trampoline. This saves energy. This foot type is very effective in an open country with firm soil and gives the animal great power of endurance. Again no transitional forms are found. The tridactyl and monodactyl horse co-occur in faunas from the Late Miocene to the Early Pleistocene. Clearly they occupied a slightly different ecological niche (Shotwell 1961, Sondaar 1968). The monodactyl horse which was better adapted to the hard soil of the plains, survived till today.

In general, the mode of locomotion in horses tends to maximize compressive stresses and minimize forces tending to bend the limbs (Camp, Smith 1942, Thomason 1985), with a consequence of stretching the legs.

Body weight and size

MacFadden (1992) suggests an increase in body size in the evolutionary sequence of fossil horses during their 58-My history from the extremes of *Hyracotherium*, with an estimated mass of 9.1 kg (MacFadden 1987) (whose size is similar to that of a fox-terrier) to *Equus* (with a mass around 500 kg, although some larger breeds may exceed 1,000 kg). However, according to Sondaar (1994) the fossil record contradicts a general increase in size from a tridactyl browser pad-footed, to the tridactyl grazer tip-toe footed and from this to the monodactyl form. On the contrary, a size decrease can be observed during the major changes in locomotion (Sondaar 1994). The change in locomotion in horses was partly a change in relative proportion due to a relative elongation of the central phalanges: the foot came off the ground and lost its pad (Sondaar 1968, 1994).

Brain capacity (Figure 2)

Edinger (1948) wrote a classic study in which she depicted the evolution of the horse brain as a gradual increase in size and complexity through time. There have been several subsequent criticisms of her work, most notably that the specimens she called *Hyracotherium* probably represented a more primitive condylarth in the same early Eocene (Watsatchian) fauna (Radinsky 1976). Regardless of this and other flaws in her work, according to MacFadden (1992) the evolution of the fossil horse brain is depicted as a clear, unidirectional trend toward increased size and complexity. However, Simpson (1951) observed a rapid change between the forest *Meshippus* and the savannah form *Merychippus*; the cerebrum, especially its neocortex, continued to increase in size and developed complex fissures; the cerebellum also became larger and more complex.

The increase can be explained by the fact that groups are more social, must have a better vision etc. So, in general in open country more skills are needed. As a consequence there will be a selection in the direction of a larger and more complicated brain.

Dentition (Figure 2)

The teeth in the forest horses were low crowned and had crests. These lophodont teeth were perfectly adapted to cut leaves and twigs. In *Parahippus*, which had already the unguligrade stand of the grazing horse, the teeth still show characters of a browser, though the occlusal surface has become more complex.

The big change can be seen a few million years later in *Merychippus*; the increase of crown height or hypsodonty and deposition of cement outside and between the enamelridges. The changes are followed gradually in the *Parahippus* and lead to completely different teeth in *Parahippus*; the hypsodont grazing teeth. In contrast to the locomotion no clear-cut changes are found in the dentition; the changes, such as increase in hypsodonty, are gradual (Spaan *et al.* 1994).

Adaptive radiation (Figure 2)

An adaptive radiation can be observed after the transformation of the locomotion and chewing apparatus had been accomplished. This radiation starts from *Merychippus/Parahippus* and its diversity is at its top in the Late Miocene, at which time about thirteen different genera of grazing horses can be distinguished. Among them is also the first monodactyl *Dinohippus*, the ancestor of the modern horse, *Equus*.

HOMINID EVOLUTION: FROM FOREST TO SAVANNAH

In general it is accepted that the environment changed from forest to savannah in the period from about 4 My – 1 My in East Africa. In this period bipedal hominids evolved (e.g. Kortlandt 1972, Coppens 1994).

Locomotion (Figure 3)**A. Apes**

Napier and Walker (in Napier 1967) distinguished a special locomotory category for the primates with very long hind limbs and very short forelimbs, which they named "vertical clinging and leaping". In this category of locomotion the mechanism permitting maintenance of the trunk in upright position is present. Napier (1967) suggests that there must have been a transition from a distant, hypothetical vertical-clinging ancestor to modern bipedal man. The transition was almost certainly marked by an intermediate quadrupedal stage. If this was knuckle-walking is a question, but at least it must have been a locomotion in which the forelimb was used as a support during quadrupedal locomotion (Washburn 1968, Corruccini 1978, Lewis 1989). The change in locomotion from the quadrupedal stage of the apes to the bipedal australopithecine locomotion evolved rapidly with no transitional forms.

B. From apes to Australopithecinae/early Homo (*habilis-rudolfensis*) (Figure 3)

The largest change is from apes to the Australopithecinae, the change from clinging and leaping to bipedal gait.

Without going into detail about the taxonomy of the early hominids, it is generally agreed, mainly based on the evidence provided by the postcranium, that the first hominids that were bipedal are members of the genus *Australopithecus sensu lato* and early *Homo* (*habilis, rudolfensis*). *Australopithecus afarensis* which lived in eastern Africa more than 3 My ago, should have had long legs and short arms relative to its size, much like modern humans (Bower 1996); according to M. Leakey (1995) *Australopithecus afarensis* had long arms like an ape, but its pelvic and leg bones indicate that it walked on two legs. The same is found in *Australopithecus africanus* which lived in southern Africa between 2.6 My and 2.8 My ago, and displayed relatively shorter legs and longer arms, more like apes (Bower 1996). The postcranium of *Homo habilis sensu stricto* remains australopithecine; some of the most conspicuous primitive traits include large forelimbs relative to hind-limbs (e.g. Johanson *et al.* 1987, Jungers 1988a, R. Leakey *et al.* 1989, Korey 1990, Hartwig-Scherer, Martin 1991). Thus, according to several authors the early members of the genus *Australopithecus sensu lato* and *Homo* are fully bipedal or terrestrial, albeit transitional between apes and man (e.g. Day 1973, Lovejoy *et al.* 1973, Lovejoy 1974, 1975, 1978, 1981, 1988, Johanson, White 1979, White 1980, Langdon *et al.* 1991). Others suggested that some features for arboreal life were retained (e.g. Tuttle 1967, 1981, Tuttle *et al.* 1991a, Robinson 1972, 1978, Zuckerman *et al.* 1973, Senut 1981, Senut, Tardieu 1985, Tardieu 1991, Susman, Creel 1979, Susman, Stern 1979, 1982, 1991, Susman *et al.* 1984, Vrba 1979, Schmid 1983, 1991, Langdon 1985, McHenry 1978, 1982, 1986, 1991a, Lewis 1989, Tobias 1991, Oxnard 1975, Oxnard, Lisowski 1980, Ashton *et al.* 1981, Rose 1984, Berge 1991, Deloison

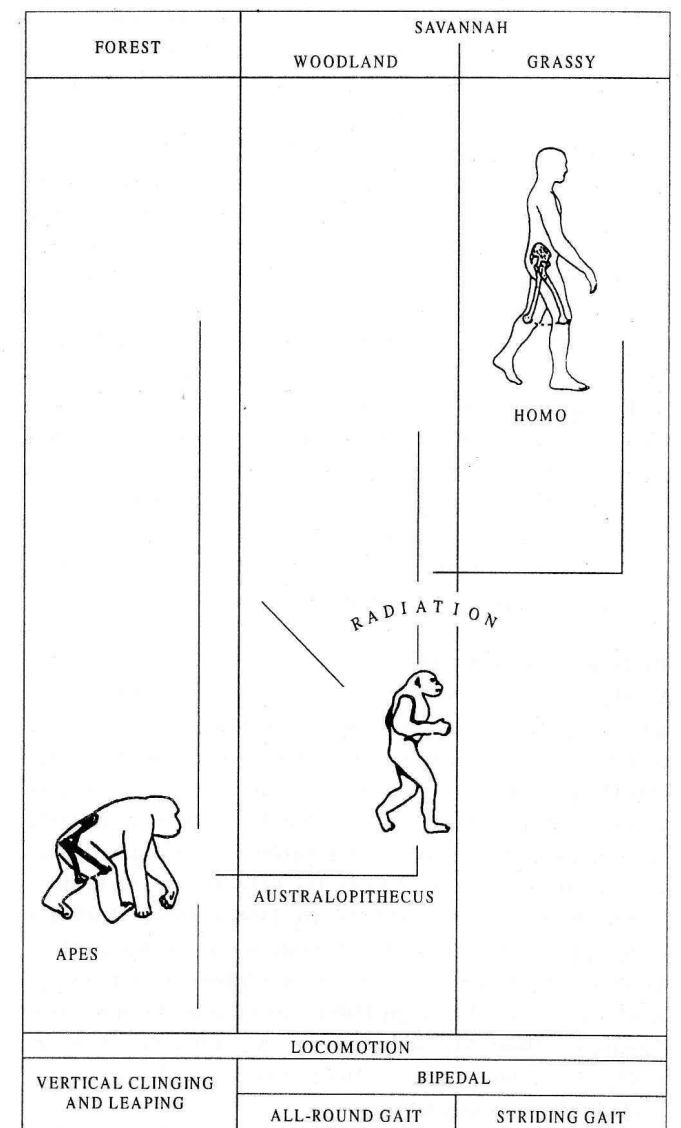


FIGURE 3. In the evolution of man there is a change from primates with a "vertical clinging and leaping" locomotion, via the forest Apes with a quadrupedal (knuckle-walking?) locomotion with a bent-hip, and a bent knee gait to the woodland savannah Australopithecinae (including *Homo habilis* and *Homo rudolfensis*) with a bipedal locomotion and an all-round gait. The latter transition must have taken place quite quickly. In the australopithecines a radiation took place. This led, among others, to the genus *Homo ergaster/erectus* with a bipedal locomotion and a striding gait.

1991, Jungers 1991, Preuschoft, Witte 1991, Spoor 1993, Clarke, Tobias 1995).

To sum up, there is a lot of discussion concerning the gait of *Australopithecus* and the early *Homo*. However, in general it can be concluded that, although the way of locomotion in the Australopithecinae/early *Homo* (*habilis-rudolfensis*) is bipedal, it is not yet the fully human striding gait. The bipedal Australopithecinae/early *Homo* (*habilis-rudolfensis*) still have a more all-round gait.

C. From Australopithecinae/early *Homo* (*habilis-rudolfensis*) to *Homo erectus* (= *ergaster*) (Figure 3)

The next stage in human evolution is *Homo erectus*, a species based on a skull-cap and a femur, found in Java (Dubois 1894). The femur clearly shows that *Homo erectus* was bipedal with the striding gait of *Homo sapiens*. This was confirmed by an almost complete skeleton of *Homo erectus* (= *Homo ergaster*) which was found in 1984 in Kenya, at Nariokotome III, West Lake Turkana (Brown *et al.* 1985). The sediments in which the skeleton was found have an estimated age of 1.6 My. The skeleton (KNM-WT 15,000) is from a male who died at an age of ± 12 years. In limb proportions and body proportions *Homo erectus* from Nariokotome was fully human (Walker, Leakey 1993), and consequently fully bipedal with a striding gait.

The transition from Australopithecinae/early *Homo* (*habilis-rudolfensis*) with a bipedal locomotion and an all-round gait to *Homo erectus* (= *ergaster*) with bipedal locomotion and a striding gait was a sudden change.

Body weight and size

McHenry (1991a, b, 1992, 1994) estimated the size of a female *Australopithecus afarensis* at about 105 cm and the weight to be approximately 29 kg. According to him (McHenry 1992, 1994) the average male size is less securely known, due to the fact that there are less complete specimens and also due to the problems associated with scaling body size and skeletal size in larger-bodied hominids. His estimate (McHenry 1991a, 1992, 1994) for male stature is 151 cm and male body weight 45 kg. Besides McHenry's estimates there are a lot of other estimates (e.g. Aiello 1992, Aiello, Dean 1990, Feldesman, Lundy 1988, Geismann 1986, Hartwig-Scherer, Martin 1991, Jungers 1988a, b, McHenry 1982, 1984, 1988) which gave more or less the same results.

McHenry (1991a, 1992, 1994) also estimated the stature of a female *Australopithecus africanus*; she was 115 cm tall and weighted 30 kg. The male may have been 138 cm high and may have weighted 41 kg. According to McHenry (1994) these are reasonable estimates, but many assumptions are required. Many other attempts are made at predicting body size of *Australopithecus africanus* (e.g. Aiello, Dean 1990, Burns 1971, Feldesman, Lundy 1988, Geismann 1986, Helmuth 1968, Jungers 1988a, b, McHenry 1974, 1975, 1976, 1988, Olivier 1976, Reed, Falk 1977, Robinson 1972, Steudel 1981, Suzman 1980, Wolpoff 1973). All are more or less similar to McHenry's estimates.

As there is no real consensus about *Homo habilis* McHenry (1991b, 1992, 1994) stated that one must appreciate the insecurity of any attempt to estimate body size. He estimated that the small, presumably female morph, had a stature of 125 cm and weighted 32 kg, while the large morph had a stature of 157 cm and weighted 52 kg.

The weight of the male early *Homo erectus* of Nariokotome may have been 68 kg and his stature 180 cm (Ruff 1991, McHenry 1991a). So, here we observe a clear

shift in body height, compared to *Australopithecus* and early *Homo*.

Brain capacity

The earliest hominids had brains with the size of modern pongids in bodies that were probably a little smaller than modern ape bodies (e.g. Pilbeam, Gould 1974, Holloway 1981a, Tobias 1981, Isaac 1983). Tobias (1994, Table 9-6) gives a table of endocranial capacities in cm³ based on Tobias (1975), Holloway (1975, 1980, 1981b) and Weidenreich (1943). This table clearly shows that there is an increase in brain capacity. According to that table the mean brain capacity of *Australopithecus afarensis* (based on 3 specimens) is about 413.5 cm³; in *Australopithecus africanus* (based on 6 specimens) it is 440.3 cm³; in *Homo habilis* (based on 6 specimens) it is 640.2 cm³; in *Homo erectus* (Asia and Africa) the mean is 937.2 cm³, ranging from 895.6–1043.0 cm³ (based on 15 specimens).

Dentition

Finally, the dentition of *Australopithecus afarensis* is of great importance: It is claimed to be significantly more ape-like than that of any other species of *Australopithecus*. In particular, the features include comparatively large incisors, frequently a unicuspid lower first premolar, a canine that is somewhat pointed with a large root and that is reminiscent of that of an ape (e.g. Johanson *et al.* 1978, Greenfield 1979, Johanson, White 1979, Wood 1981). It also shows noticeable sexual dimorphism. It is associated with a small diastema in the upper jaw.

This indicates a change in diet at the transition from forest to a more open woodland-savannah. This implies a change in chewing apparatus. *Australopithecus afarensis*, which has well developed incisors, could still have had much fruit in his diet, while *Australopithecus africanus*, the gracile form, with lower canines, might probably also have eaten meat in addition to vegetarian food. The robust form had a strictly vegetarian diet.

Adaptive radiation

When the hominids entered into the new environment of the woodland-savannah, an adaptive radiation took place in the australopithecines (e.g. Robinson 1962) and early *Homo*.

Several species are distinguished, although there is a discussion about the validity of those species. The following species of *Australopithecus* and *Homo* are found in the literature:

- The early forms *Australopithecus anamensis*, *Australopithecus bahrelghazali* (around 4 My ago) and *Australopithecus afarensis* (from about 4 to 3 My ago);
- the gracile form *Australopithecus africanus* (from about 3 to 2.3 My ago);
- the robust forms of *Australopithecus* (*Paranthropus*) *aethiopicus* (from about 2.6 to 2.2 My ago), *Australopithecus* (*Paranthropus*) *boisei* (from about 2.6 to 1 My ago), and *Australopithecus* (*Paranthropus*) *robustus* (from about 2 to 1.2 My ago);

- the early *Homo*: *Homo habilis* (from about 2.6 to 1.9 My ago) and *Homo rudolfensis* (from about 2.5 to 1.6 My years ago).

TAXONOMY OF EQUIDS AND HOMINIDS

With the classification of the Equidae, mainly the dental characters are used; it was/is a general practice to put the genus *Parahippus*, based on the dental characters, in the subfamily of the Anchitheriinae (Stirton 1940, Simpson 1945, 1951, MacFadden 1992). According to Sondaar (1969) there is a big difference between the post-cranial skeleton of *Parahippus* and that of the Anchitheriine group, and he stated that *Parahippus* must be attributed to the Hipparionae.

Mainly the locomotion is crucial to enter a new adaptive niche, and this then must be decisive for the taxonomy.

The same holds true for the hominids. The classification of hominids is mainly based on the brain capacity. To include the first specimen from Olduvai, which had a little larger brain capacity than *Australopithecus*, within the genus *Homo*, L. Leakey *et al.* (1964) had to revise the diagnosis of this genus; hominids with a brain capacity over 600 cm³ were considered to belong to *Homo*.

In brain capacity *Homo habilis* lies above the average of the Australopithecinae (640.2 cm³), but is closer to this group (413.5–440.3 cm³) than to *Homo erectus* (895.6–1043.0 cm³).

A partial skeleton of an adult hominid from lower Bed I (about 1.8 My ago), Olduvai Gorge, indicates attribution to *Homo habilis* with regard to cranial anatomy, but its postcranial anatomy, including small body size and relatively long arms, is strikingly similar to that of some early *Australopithecus* individuals (Johanson *et al.* 1987). So, in locomotion it belongs clearly to the Australopithecinae.

In this case it is better, based on the postcranials, to attribute the early *Homo* species, *habilis* and *rudolfensis*, to the genus *Australopithecus*.

Just as in the horse the rapid evolutionary shift in locomotory apparatus enables the hominid to enter a new environment. This clear morphological marker needs to be used for taxonomy and not that of arbitrary one of taxa occupying most probably the same ecological niche. Just as *Parahippus* is in locomotion not an anchitherine horse, but a tiptoed tridactyl one, in locomotion *Homo habilis* is not a *Homo* species but one of the Australopithecinae.

A NEW SCENARIO FOR BIPEDALISM IN HOMINIDS

The consequence of change in habitat, from forest to open savannah, was the need to cover larger distance on a "flat plain" in search for food.

From the evolutionary history of the horse we can learn that they evolved a system that avoids large muscle tension by keeping their legs more stretched than small and subcursorial mammals. Small mammals run with their legs bent and large mammals keep their legs stretched; the difference is a matter of body proportions. Biomechanics show that the method of running of large mammals is relatively more economical than that of small mammals. That is why the size may increase almost without extra energy to be invested in the locomotion. From above there can be deduced that the evolution of the horse demonstrates an evident relation between functional morphological changes and changes in the environment. The change from the forest to the plains is marked by major evolutionary changes. The horse evolved a locomotion in which speed and endurance are combined and a chewing mechanism with high crowned teeth adapted to grind hard grasses found in the dry plains. The first horses that entered the open environment evolved a tiptoe unguligrade hoofed foot, still tridactyl, which gave them a degree of all roundness. After entering the plain there was a gradual selection on brain size and dentition, because of the dietary change and the more complicated skills that are needed in the open environment. Evidently this horse found many new niches, radiation in this tiptoed tridactyl grazing horse was the result. Finally the monodactyl horse evolved.

A similar evolutionary pattern as in horses can be observed in hominids. In apes the locomotion is strongly focused on the hind legs; the forelimb is used as a support during quadrupedal locomotion. It is not a surprise that a selection concentrated on the posterior extremities, with upright walking as a consequence. Walking in an upright position, with stretched legs had an important consequence; this way of locomotion carries the body-weight without the use of much stress in the leg muscles. The "power cost" and thus the amount of energy spent, will be strongly reduced (McNeill 1992). Biomechanics demonstrate that walking in an upright position is energetically more efficient than the locomotion of the great apes. In the hominids this was acquired by a selection for bipedal locomotion, first with an all-round gait. Subsequently a change in dentition, an increase in the brain capacity, and an increase in body size took place. Entering the new environment they found many open niches; a radiation could taken place. Later the bipedal locomotion with the striding gait in *Homo ergaster/erectus* evolved and this may be considered as very effective, in the sense of endurance, just like the monodactyl horse.

CONCLUDING REMARKS

The question "Why did the hominids become bipedal?" must be rephrased in "Why did the locomotion with stretched legs originate?". This question can be answered for the horse as well as for the hominids. A locomotion in which endurance played an important role and that did not

cost much energy was the best adaptation for the open environment.

The evolution of the hominoids and horses proceed according to comparable patterns:

1. Punctuated in locomotion and gradual in the cranial characters;
2. A radiation in different morphotypes followed after punctuated evolution as the pioneer structure, bipedal locomotion in the hominoids and the tip-toe in the horse, and subsequent entering the open plain.

From this it may be concluded that there was not any fundamental difference in evolution between humans and the horse. Also the explanations of the evolutionary changes can be provided in a similar way and reflect an adaptation to the changing environment.

Not only in horse but also in humans the pattern of evolutionary change causes a problem in taxonomy. Depending on morphology, there is an inconsistency in taxonomy:

- a taxonomy in which gradual changes of the cranial morphology are the starting point;
- a taxonomy in which the punctuated changes in locomotion are used as reference point to distinguish different genera.

In our opinion the punctuated changes in locomotion, which are pioneer structures and enable the taxa to enter a new environment, must be reflected in the taxonomy and not the arbitrary gradual changes of the cranium. In *Homo* the striding gait distinguishes it from the all-round gait in *Australopithecus*. In this case the species *habilis* must be attributed to the genus *Australopithecus*, as it still has an all-round gait and the boundary on cranial capacity is highly arbitrary.

The evolution in hominids follow parallel patterns seen in other mammals and is not unique. It needs to be treated as such. *Homo* is just "another unique species" (Foley 1987).

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